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Abstract

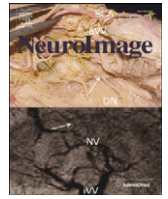
In a highly dynamic visual environment the human brain needs to rapidly differentiate complex visual patterns, such as faces. Here, we defined the temporal frequency tuning of cortical face-sensitive areas for face discrimination. Six observers were tested with functional magnetic resonance imaging (fMRI) when the same or different faces were presented in blocks at 11 frequency rates (ranging from 1 to 12 Hz). We observed a larger fMRI response for different than same faces – the repetition suppression/adaptation effect – across all stimulation frequency rates. Most importantly, the magnitude of the repetition suppression effect showed a typical Gaussian-shaped tuning function, peaking on average at 6 Hz for all face-sensitive areas of the ventral occipito-temporal cortex, including the fusiform and occipital “face areas” (FFA and OFA), as well as the superior temporal sulcus. This effect was due both to a maximal response to different faces in a range of 3 to 6 Hz and to a s...

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Temporal frequency tuning of cortical face-sensitive areas for individual face perception



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ABSTRACT

In a highly dynamic visual environment the human brain needs to rapidly differentiate complex visual patterns, such as faces. Here, we defined the temporal frequency tuning of cortical face-sensitive areas for face discrimination. Six observers were tested with functional magnetic resonance imaging (fMRI) when the same or different faces were presented in blocks at 11 frequency rates (ranging from 1 to 12 Hz). We observed a larger fMRI response for different than same faces – the repetition suppression/adaptation effect – across all stimulation frequency rates. Most importantly, the magnitude of the repetition suppression effect showed a typical Gaussian-shaped tuning function, peaking on average at 6 Hz for all face-sensitive areas of the ventral occipito-temporal cortex, including the fusiform and occipital “face areas” (FFA and OFA), as well as the superior temporal sulcus. This effect was due both to a maximal response to different faces in a range of 3 to 6 Hz and to a sharp drop of the blood oxygen level dependent (BOLD) signal from 6 Hz onward when the same face was repeated during a block. These observations complement recent scalp EEG observations (Alonso-Prieto et al., 2013), indicating that the cortical face network can discriminate each individual face when these successive faces are presented every 160–170 ms. They also suggest that a relatively fast 6 Hz rate may be needed to isolate the contribution of high-level face perception processes during behavioral discrimination tasks. Finally, these findings carry important practical implications, allowing investigators to optimize the stimulation frequency rates for observing the largest repetition suppression effects to faces and other visual forms in the occipito-temporal cortex.

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Introduction

In everyday life the human brain is constantly presented with many different faces (e.g., when walking in a crowd). It is able to differentiate these faces very rapidly, even when they have never been seen before (i.e., unfamiliar faces). Neuroimaging studies have investigated individual face discrimination by taking advantage of the phenomenon of repetition suppression, also called fMRI adaptation (Grill-Spector and Malach, 2001; Grill-Spector et al., 2006). Specifically, the reduction of the fMRI signal for repeated compared to different faces in the fusiform gyrus, and more posteriorly in the lateral occipital complex, points to the involvement of face-sensitive areas in individual face discrimination (e.g., Davies-Thompson et al., 2009; Gauthier et al., 2000; Grill-Spector and Malach, 2001; Grill-Spector et al., 1999).

In the present study, we investigated the temporal rate at which individual faces can be discriminated in functional brain areas that respond more to pictures of faces than nonface objects (“face-sensitive areas”, Haxby et al., 2000; Puce et al., 1995; Sergent et al., 1992). This issue is important because humans live in a highly dynamic visual world in which they are exposed to many different faces within a short timeframe, or even simultaneously. Therefore, being able to rapidly individualize faces may be critical for adequate social interactions. Moreover, face-sensitive areas along the cortical visual hierarchy may have different temporal frequency tuning functions, which may shed light on their respective contribution to face perception.

Most neuroimaging studies that have addressed the issue of temporal frequency tuning have used low-level stimuli such as flickering pattern-flashes (Pastor et al., 2003), checkerboards (Fox and Raichle, 1984, 1985), gratings (Muthukumaraswamy and Singh, 2008; Singh et al., 2000) or chromatic versus achromatic simple stimuli (D’Souza et al., 2011; Liu and Wandell, 2005; Mullen et al., 2010). Using object shapes, Mukamel et al. (2004) reported a significant but relatively lower signal increase in high-level as compared to low-level areas when the stimulation rate of face and house stimuli increased from

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1 Hz to 4 Hz. Above 4–5 Hz, a decline of temporal frequency tuning to faces in category-sensitive high-level visual areas such as the “fusiform face area” (FFA, Kanwisher et al., 1997) has been reported in two studies (Gauthier et al., 2012; McKeef et al., 2007).

Here, the temporal frequency tuning of individual face discrimination was investigated by studying the repetition suppression effect across many stimulation frequency rates. To our knowledge, the frequency tuning of repetition suppression has never been determined, whether low-level or high-level visual stimuli are concerned. Specifically, we measured fMRI responses to face stimuli presented at multiple frequency rates (1–12 Hz) in two conditions of interest, namely repetition of the exact same face during a block or different faces, and we computed the response difference between these two conditions. We focused our investigation on the whole set of face-sensitive areas identified in an independent whole-brain functional face localizer (Rossion et al., 2012). In line with independent results obtained with scalp electroencephalogram (EEG) concerning both frequency tuning (Alonso-Prieto et al., 2013) and the time course of individual face repetition effects (Jacques et al., 2007), we hypothesized a maximal neural adaptation effect at 6 Hz on average, expecting a decrease of the peak of the frequency tuning function along the cortical hierarchy of face-sensitive areas.

Methods

Subjects

Six healthy volunteers (4 females) with normal visual acuity participated in the main experiment and performed two fMRI sessions. Due to the large amount of different points sampled in the parametric design (11 frequencies \times same/different faces, see *Procedure*) and to the specific hypotheses about the tuning function of the responses to multiple temporal frequencies (see *Introduction*), a rather limited number of participants was tested in two fMRI sessions. All participants were undergraduate students (mean age = 23.5 \pm 2.3) recruited at Maastricht University. Their participation was compensated with cash money. After the explanation of the procedures, participants signed an informed consent form. The ethical committee of the faculty (Ethical Committee Psychology, ECP) approved the study.

Stimuli

The stimuli consisted of 18 different faces (males in the first 2 runs and females in the remaining 3 runs). In 2 runs (out of 5) we used a set of face pictures from the Tubingen Max Planck Institute (MPI) database of laser-scanned (Cyberware TM) heads. For the remaining 3 runs, faces were selected from a large set of pictures used in a recent behavioral study (Laguesse et al., 2012). The pictures were in color, they were all taken under similar lightning with neutral facial expressions and they were additionally equalized in luminance. Faces were presented on a light-gray background and were unfamiliar to the participants.

Procedure

Face stimuli were presented in blocks and were repeated with a variable stimulation rate ranging from 1 Hz (1 face per second) to 12 Hz (12 faces per second = one face every 83.33 ms). Specifically, faces were presented at 11 different frequencies: 1, 2, 3, 4, 5, 6, 6.66, 7.5, 8.57, 10, and 12 Hz. These rates were selected to cover a wide range of stimulation frequencies with a fine-grained sampling, and were constrained by the refresh rate of the stimulation monitor (i.e., 60 Hz/frequency rate = integer). Faces were presented according to a sinusoidal contrast-modulation function, i.e., every cycle started with a gray background changing sinusoidally into a face stimulus, which reached its full contrast at half a cycle (Fig. 1.c, see Rossion and Boremanse, 2011). Compared to a boxcar ON/OFF function, the sinusoidal function makes the face stimulus appear and disappear more smoothly, and has been successfully used in

recent EEG studies to elicit robust periodic visual responses to faces (Rossion and Boremanse, 2011). Specifically, the first sample of a cycle consisted of a face with 0% contrast, at half a cycle the face was presented at full contrast and the last sample was again a 0% contrast stimulus. It follows that for high frequency rates, the number of samples per cycle is smaller compared to low frequency rates. However, as a face is clearly visible at 30–35% of contrast, even at 12 Hz (5 samples per cycle at a 60 Hz refresh rate of the monitor) there are 4 consecutive samples at which the face is visible (40%–80%–80%–40%). Therefore, it is reasonable to assume that also for very high frequencies, most of the samples per cycle represented “perceivable” faces. The stimuli were delivered in Matlab (the Mathworks) via a custom-made application (SinStim) whose timing accuracy was verified by an oscilloscope and validated by the frequency spectrum analysis of a similar EEG study.

The faces in a block were either identical (same) or different from each other (Fig. 1.b). In each block where the same face was presented repeatedly, the program selected one of the 18 faces, randomly. In the blocks of different faces, all of the 18 faces were presented in random order, with the constraint that a given face was never presented twice consecutively. Thus, the complete design consisted of a total of 22 conditions: 11 frequencies \times same/different faces (Fig. 1.a). An automatic algorithm ensured that the order of those conditions was randomized for every run.

The participants performed 5 runs in total (spread over two fMRI recording sessions to include the functional localizer runs, see the next section, *Localization of face-sensitive areas*), each consisting of 22 blocks (one block per condition). A run started with a blank screen lasting for 18 s after which the first block-condition was presented. A single block lasted for 27 s and it was followed by a resting period of 9 s. During a block of faces the participant was instructed to attend to a black cross that was positioned at the level of the nasion of the face (roughly corresponding to the center of the screen). In order to keep the participants' attention high and constant during a block of faces, they were asked to press a response key when the black cross turned red (between 2 and 3 times during a block and in a random position within the block). Moreover, in order to eliminate low-level repetition suppression effects, the faces changed randomly in size (88–112% of a base face) at every cycle. A base face size subtended approximately 9.1° (height) \times 6.3° (width) of visual angle (8.0° \times 5.5°–10.2° \times 7.0°) and was aligned with the center of the screen. The participants were not made aware of any of the manipulations described. The entire session lasted approximately 60 min.

Localization of face-sensitive areas

An independent functional localizer, fully described in a recent study (Rossion et al., 2012), was used to localize the face-sensitive areas in each individual brain. This localizer consisted of 4 different categories of stimuli photographs: faces, cars, scrambled faces and scrambled cars. The original photographs of the face stimuli were edited to eliminate external features (e.g., hair). Both the face and car categories consisted of 43 different stimuli (22 of the 43 faces were female), they were presented in color, in frontal view and embedded in a gray rectangle. Scrambled faces and scrambled cars were made by applying a Fourier phase randomization procedure. This algorithm replaces the phase spectrum related to the Fourier transformation of the face and car stimuli with random values while keeping the amplitude spectrum of the image unaltered (Nasanen, 1999). This procedure degrades completely category-related information and yields images that preserve the global low-level properties of the original image (luminance, contrast, spectral energy, etc.). The pictures of the 4 categories of stimuli subtended equal shape, size and contrast against background.

The participants performed 3 runs, each lasting for 11 min. The 4 different categories of stimuli were presented in blocks. In a single run 6 blocks were presented per category, for a total of 24 blocks. Each block lasted for 18 s and 24 stimuli were presented in each block (no resting

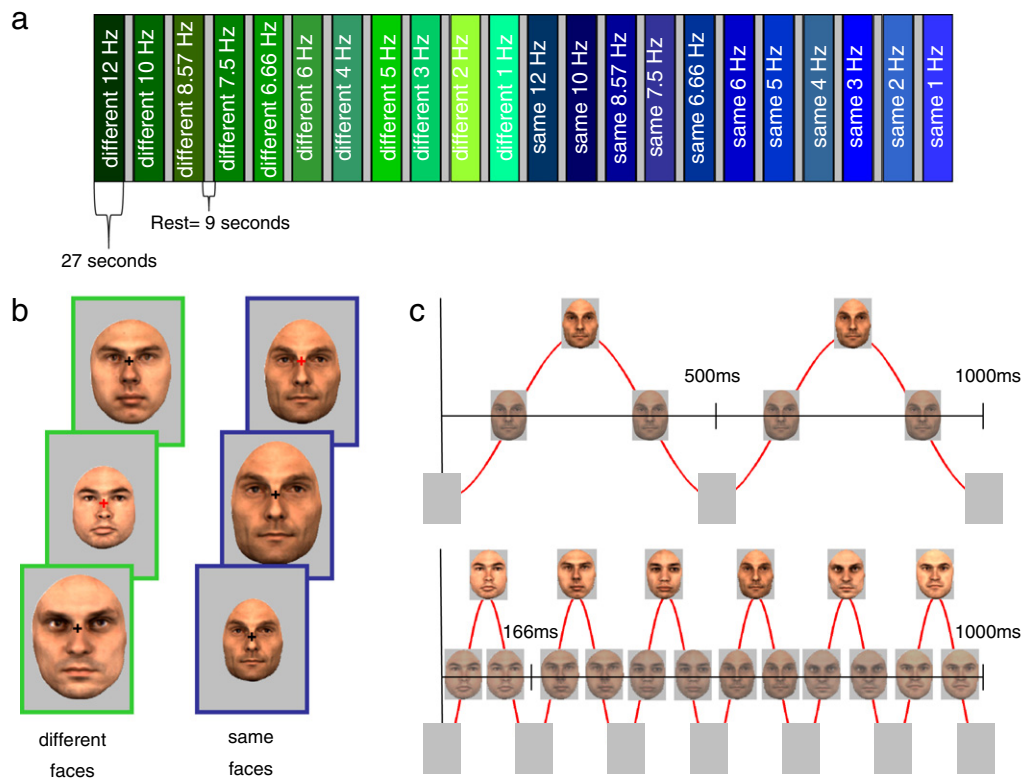


Fig. 1. Experimental design. a) Example of the experimental paradigm of a single run. A run consisted of 22 blocks of trials and 22 different conditions (1 block per condition). Each block lasted for 27 s and two blocks were separated by a resting period of 9 s. b) Example of the stimuli presented in the different and same faces condition. The size of the face changed at every trial. A black cross was presented on the top of the nose of each face. The task of the subject was to press a button when the color of the cross turned red. c) Two examples of the type of face-trial presentation within 1 s. Top: two cycles of the same faces condition at 2 Hz. Bottom: six cycles of the different faces condition at 6 Hz.

condition was interleaved between two consecutive stimuli); the duration of each stimulus in a block was 750 ms. Within a block, the same stimulus could be consecutively repeated 2 or 3 times. The stimulus size was 6.2° (height) \times 5.5° (width) of visual angle and stimuli were presented centrally. In order to control that a specific element belonging to the face/car stimuli (e.g., the eyes or headlights) were not shown at the same location in two consecutive trials, the stimulus location randomly varied from the central location horizontally (6%) and vertically (8%) at each presentation. Blocks were separated by a rest condition lasting for 9 s and consisting of a centrally located cross on a black background. The subjects were asked to detect the immediate repetition of a given stimulus (one-back task) over the duration of the entire run (2 or 3 targets per block; 30 targets for each condition in total).

Data acquisition

Images were acquired on a 3 T Siemens Magnetom Allegra head scanner (Siemens Medical System, Erlangen, Germany) using a standard head coil. Thirty-six oblique axial slices (in-plane resolution: $3.5 \text{ mm} \times 3.5 \text{ mm}$, slice thickness: 3.5 mm, interslice distance 0 mm) covering the entire cortical volume were acquired using an echo planar imaging sequence (repetition time (TR) = 2250 ms, echo time (TE) = 30 ms, matrix: 64×64). For each run of the main experiment and the functional localizer, 356 and 293 volumes were respectively acquired. The first two volumes were discarded from the analysis due to the T1 saturation effect. Functional slices were aligned to a high-resolution 3D anatomical dataset acquired in the middle of the entire session and consisting of 192 slices (ADNI sequence: TR = 2250 ms; TE = 2.6 ms; flip angle = 9° , voxel dimension = $1 \times 1 \times 1 \text{ mm}^3$).

The participants were placed comfortably in the scanner and their heads were fixated with foam pads. They saw the stimuli projected on

a screen through a mirror mounted on the head coil. The visual stimulus was perceived at a distance of 57 cm.

Analysis

Both the functional and the anatomical data were analyzed using the BrainVoyager QX package 2.2.1 (Brain Innovation B.V., Maastricht, The Netherlands). The anatomical scans were used to project the statistical results from the functional data onto high-resolution anatomical images. They were also used to derive the Talairach coordinates needed to normalize both sets of data.

Functional data were pre-processed, aligned to the anatomical images and normalized. The pre-processing procedure started with correcting the data for motion artifacts in three dimensions and for slice scan-time differences. Subsequently, linear drifts were removed from the signal and data were high-pass filtered to remove slow frequency drifts of up to 2 cycles per time course. After the pre-processing, functional data were aligned to the high-resolution anatomical images and normalized to the standard 3-dimensional Talairach space. The final version of the functional data consisted of a 4-dimensional (x, y, z, and t) dataset in Talairach space for each run and participant.

Following brain normalization, face-localizer functional runs were analyzed for each individual brain. A standard General Linear Model (GLM) analysis was performed with the 4 stimulus types (faces, cars, scrambled faces and scrambled cars) as predictors. The localization of face-sensitive areas consisted of several steps. First, a conjunction analysis between faces vs. objects and faces vs. scrambled faces was performed (Rossion et al., 2012). Clusters of voxels that were statistically significant after correction for multiple comparison via the false discovery rate approach ($\text{FDR} - q(\text{FDR}) < .05$) (Genovese et al., 2002) were selected. In order to define the final set of face-sensitive areas, anatomical

landmarks were also used (Weiner and Grill-Spector, 2010). In particular, we focused on the core system of the face-sensitive network (Haxby et al., 2000): the middle fusiform gyrus and the lateral part of the inferior occipital lobe where FFA and the occipital face area (OFA) are located, as well as the posterior part of the superior temporal sulcus (pSTS) (e.g., Haxby et al., 2000; Ishai, 2008; Rossion et al., 2012; Weiner and Grill-Spector, 2010).

With regard to the analysis of the main experiment, this was restricted on the functionally defined face-sensitive areas (see above). A GLM analysis with 22 predictors (11 frequencies \times same/different faces) was used to estimate the corresponding beta values (summary statistics) for each subject ($N = 6$). These values were then entered as dependent variables in a factorial ANOVA, with identity-repetition (2 levels) and frequency (11 levels) as factors, in order to assess the main effects of adaptation and frequency and their interaction. Next, different and same conditions were scaled from 0 to 1 in order to isolate the effect of frequency from the general effect of identity-repetition and to control for any inter-subject variability related to the different and same conditions. Then, the difference between the betas associated with the same and different conditions were computed and a one-way ANOVA (with the single factor frequency: 11 levels) was performed only on the face-sensitive regions that showed both main effects and a significant interaction in the previous analysis. In order to examine the hypothesis that face adaptation peaks at 6 Hz we

performed a Fisher's least significant difference (LSD) procedure on those areas that showed a significant main effect of frequency. In particular, we compared the mean beta related to 6 Hz against the betas associated with all the other frequencies.

Finally, our analysis was extended beyond the cortical face network to assess repetition suppression effects at the level of the whole brain. In order to accomplish this goal, a FFX GLM analysis with 22 predictors (11 frequencies \times same/different faces) was performed. In this approach, participants (6) and runs (5) were collapsed together and the beta values associated with predictors were independently estimated for each voxel. The brain areas sensitive to repetition suppression for each temporal frequency rate were identified by running a statistical conjunction among the contrasts resulting from the different vs. same faces condition for each frequency (11 in total). This analysis was corrected for multiple comparisons by using FDR (q (FDR) $< .05$). The significant clusters entered the same statistical analysis described above for the face-sensitive areas.

Results

Face localizer

Each of the 6 subjects showed a total of 7 face-sensitive regions. Four of those were located within the core section of the face-sensitive network (see *Localization of face-sensitive areas* and Fig. 2): the right OFA,

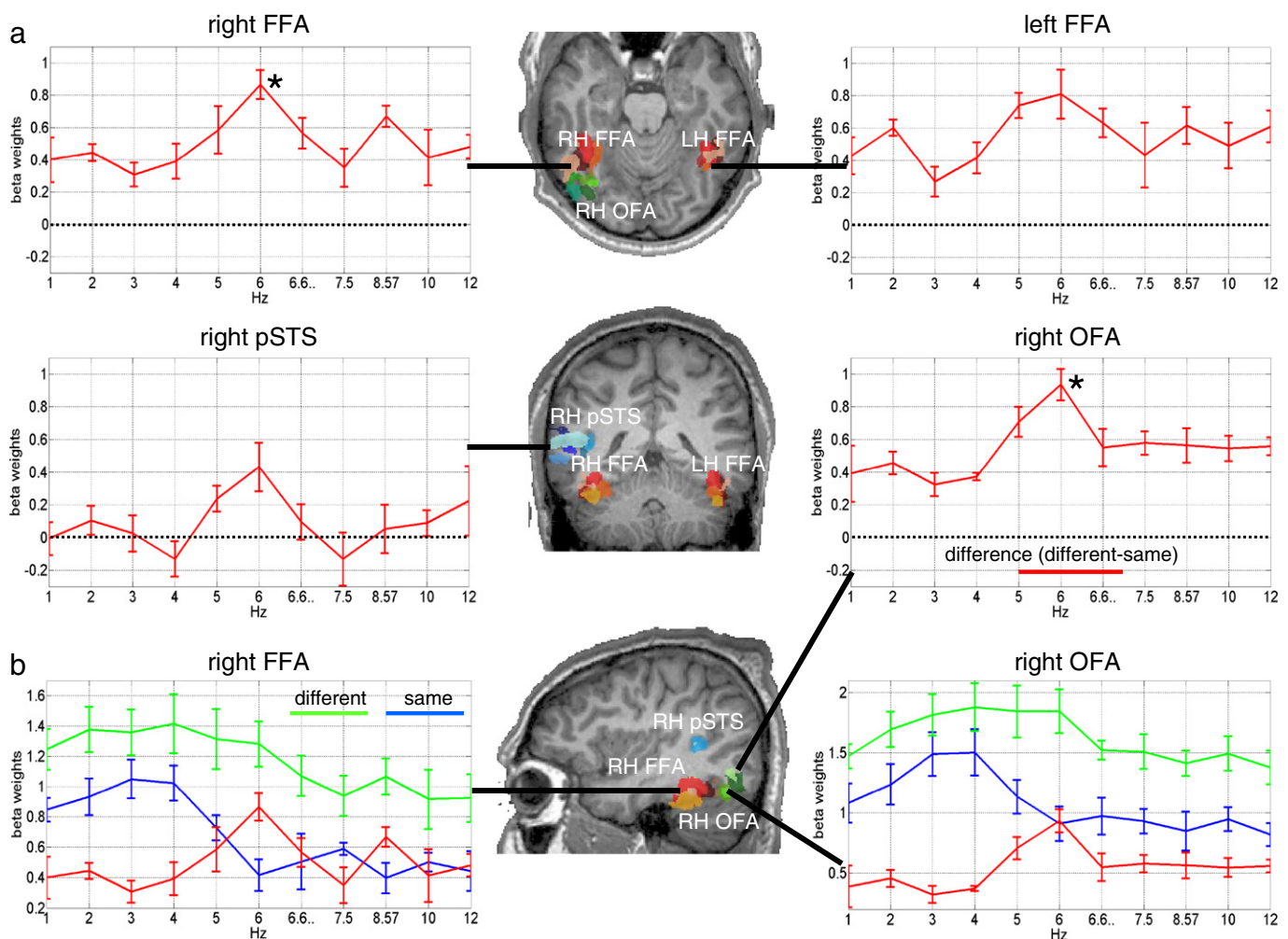


Fig. 2. Results of the ROI analysis performed within the 4 core face-sensitive areas. a) Beta weights (extracted from the GLM analysis) related to the difference between the different and same faces conditions across frequencies for all 4 areas. The 6 different tones of red associated with the right and left FFA are related to the right and left FFA of the 6 different subjects. The same rationale was applied for the right OFA (tones of green) and for the right pSTS (tones of blue). The asterisk in correspondence of 6 Hz for the right FFA and the right OFA represents the significant difference between the adaptation effect at 6 Hz in comparison to all other frequencies. b) Beta weights (extracted from the GLM analysis) related to different and same faces conditions, and to the difference between the two conditions for the right OFA and right FFA.

right FFA, the left FFA and right pSTS. The remaining 3 areas were included in the final analysis because their selectivity for faces was consistently observed in all the subjects. They were located in the anterior part of the inferior temporal cortex (aIT) in the right hemisphere and bilaterally within the early visual cortex. We defined the latter spots as the “posterior face areas” (pFA).

Main experiment

The fMRI response related to the same and different faces conditions showed a typical BOLD-like shape function for all of the face-sensitive areas (e.g., right OFA in Fig. 3), with a larger response for the different than the same faces. Strikingly, in the same areas and in particular within the bilateral FFA, right OFA and right pSTS, the BOLD response difference between the different and the same faces had a Gaussian-shaped function, with a distinct peak at 6 Hz (Fig. 2).

The outcome of the statistical analysis is reported in Table 1. There was a main effect of frequency in all core areas of the face-sensitive network (i.e., the right OFA, right FFA, left FFA and right pSTS). Moreover, both the main effect of adaptation and the interaction between identity-repetition and frequency were significant for the right OFA and the bilateral FFA (Table 1.a). For these latter areas the identity-repetition \times frequency interaction was further investigated (see Analysis). Both the right OFA and the right FFA showed a significant

effect of frequency for the difference-betas. A post-hoc LSD test revealed that this difference (adaptation effect) was significantly larger at 6 Hz than at all the other frequencies, for both areas (Table 1.b; Fig. 4 for individual data for FFA). At the frequency rate of 6 Hz, the difference of activation between the different and same faces conditions reached 0.866 and 0.935 in terms of % BOLD signal change in the right FFA and OFA, respectively.

With regard to the additional face-sensitive areas, namely the right aIT and the bilateral pFAs, there was also a main effect of identity-repetition for all 3 regions. There was a main effect of frequency only for the right aIT and the right pFA. Finally the interaction effect between identity-repetition and frequency was significant for the right pFA and for the left pFA. In summary, among the 3 additional face areas only the right pFA showed a main effect of identity-repetition and frequency and an interaction between the two factors. Therefore, this area underwent the one-way ANOVA (see Analysis) with frequency as the only factor. This analysis did not show any significant result (Table 1.a).

The individual face identity-repetition effect was also investigated in the whole brain, independent of any functional localization. This whole brain analysis revealed 4 different clusters consisting of 2 pairs of symmetrical spots in both hemispheres (q (FDR) $< .05$). They were located in correspondence to the middle fusiform gyrus (right: $x = 35$, $y = -47$, $z = -20$; left: $x = -39$, $y = -51$, $z = -22$) and in another region on the boundary between the posterior fusiform gyrus and the

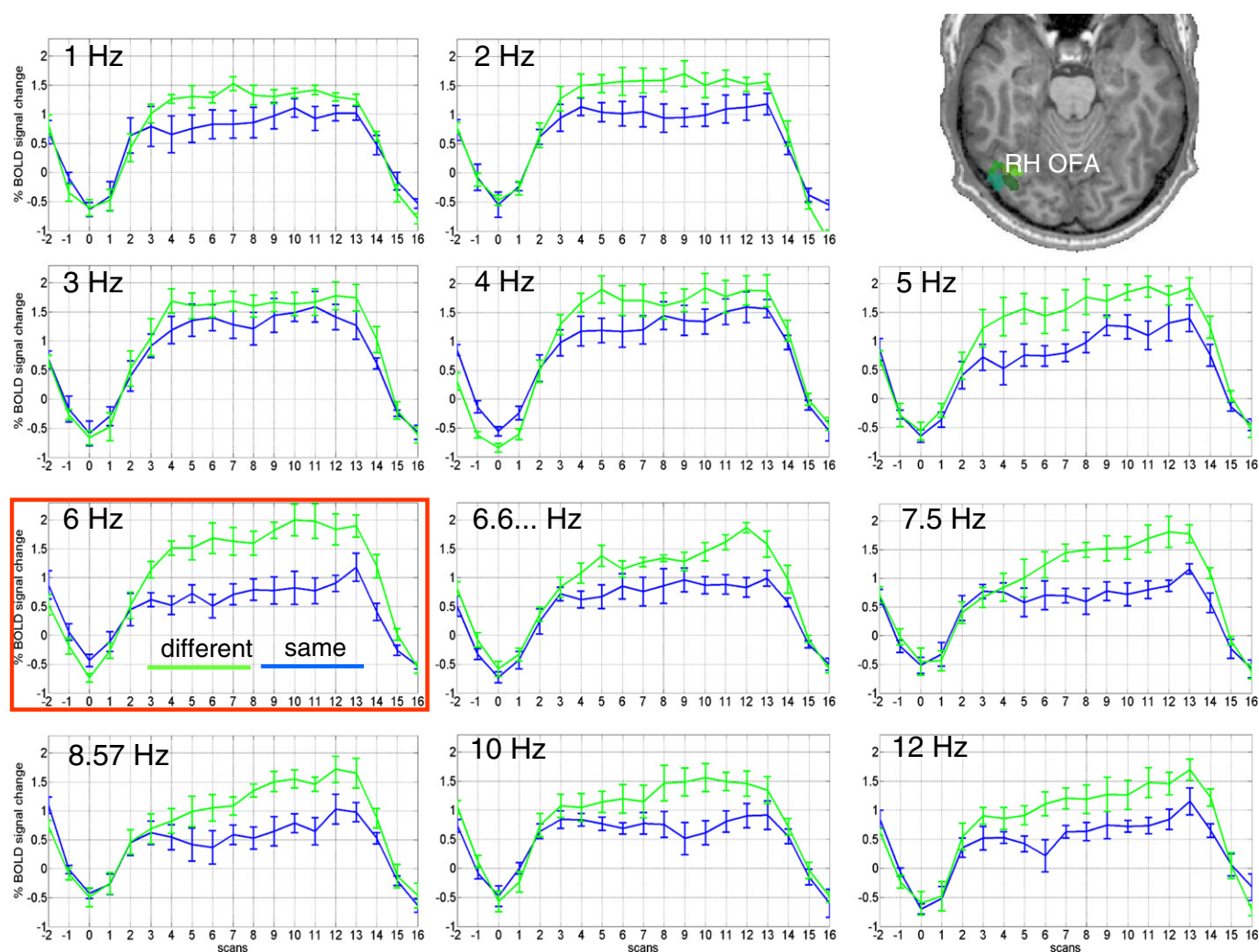


Fig. 3. Percent of BOLD signal change over time (averaged across 5 repetitions and 6 participants) measured in the right OFA related to the different and same conditions separately displayed for each frequency rate. The graph underlined in red corresponds to the 6 Hz frequency that significantly showed the largest difference between different and same conditions among all the frequencies.

Table 1

Results from the statistical analysis. a) Regions of interest, corresponding locations in Talairach coordinates and number of voxels. From left to right the main effect of frequency, adaptation and interaction between the two factors are respectively shown. The last column represents the main effect of frequency related to the scaled data. b) LSD test performed on the right OFA and right FFA. The comparisons between the adaptation effect at 6 Hz against all the others frequencies are shown.

a)								
	X	Y	Z	Nr voxels	Frequency	Adaptation	Interaction	Frequency (scaled)
RH pFA	31	−86	−14	521	$F(10, 50) = 2.142$ $p = .038$	$F(1, 5) = 19.052$ $p = .007$	$F(10, 50) = 2.252$ $p = .029$	$F(10, 50) = 1.529$ $p = .157$
RH OFA	40	−67	−18	525	$F(10, 50) = 9.658$ $p = .000$	$F(1, 5) = 255.946$ $p = .000$	$F(10, 50) = 3.474$ $p = .002$	$F(10, 50) = 3.244$ $p = .003$
RH FFA	40	−45	−23	1755	$F(10, 50) = 10.090$ $p = .000$	$F(1, 5) = 74.808$ $p = .000$	$F(10, 50) = 2.796$ $p = .008$	$F(10, 50) = 3.232$ $p = .003$
RH aIT	34	−8	−28	626	$F(10, 50) = 2.963$ $p = .005$	$F(1, 5) = 12.046$ $p = .018$	$F(10, 50) = 1.495$ $p = .169$	
RH pSTS	51	−43	4	810	$F(10, 50) = 3.884$ $p = .001$	$F(1, 5) = 3.799$ $p = .109$	$F(10, 50) = 1.701$ $p = .107$	
LH pFA	−30	−84	−16	410	$F(10, 50) = .813$ $p = .617$	$F(1, 5) = 50.265$ $p = .001$	$F(10, 50) = 3.121$ $p = .004$	
LH FFA	−42	−46	−23	1353	$F(10, 50) = 5.674$ $p = .000$	$F(1, 5) = 64.046$ $p = .000$	$F(10, 50) = 2.486$ $p = .017$	$F(10, 50) = 2.075$ $p = .045$
b)								
RH OFA	6 Hz > 1 Hz: $p = .016$; 6 Hz > 2 Hz: $p = .000$; 6 Hz > 3 Hz: $p = .000$; 6 Hz > 4 Hz: $p = .000$; 6 Hz > 5 Hz: $p = .002$ 6 Hz > 6.66 Hz: $p = .033$; 6 Hz > 7.5 Hz: $p = .002$; 6 Hz > 8.57 Hz: $p = .037$; 6 Hz > 10 Hz: $p = .003$; 6 Hz > 12 Hz: $p = .000$							
RH FFA	6 Hz > 1 Hz: $p = .007$; 6 Hz > 2 Hz: $p = .001$; 6 Hz > 3 Hz: $p = .000$; 6 Hz > 4 Hz: $p = .001$; 6 Hz > 5 Hz: $p = .048$; 6 Hz > 6.66 Hz: $p = .03$; 6 Hz > 7.5 Hz: $p = .000$; 6 Hz > 8.57 Hz: $p = .045$; 6 Hz > 10 Hz: $p = .004$; 6 Hz > 12 Hz: $p = .001$							

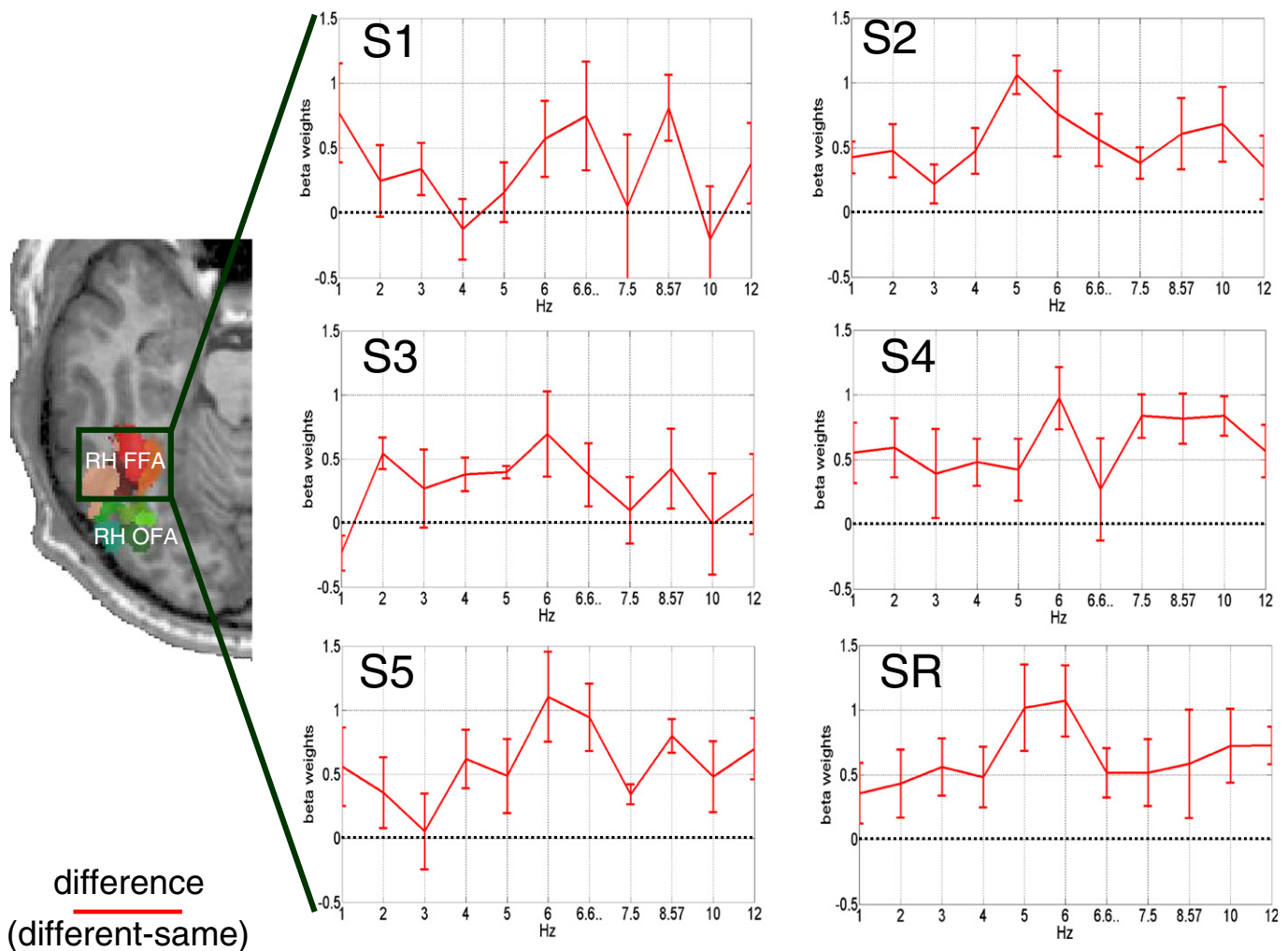


Fig. 4. Region of interest analysis in the right FFA separately for each subject. Beta weights (extracted from the GLM analysis) related to the difference between different and same condition across frequencies. The different tones of red color represent the location of the right FFA for the 6 subject.

inferior/middle occipital gyrus (right: $x = 40, y = -68, z = -16$; left: $x = -40, y = -71, z = -17$). These areas clearly overlap with the FFAs and OFAs previously described (Table 1 and Fig. 5.b). For this reason, interaction between identity-repetition and frequency was not analyzed further within these areas. For the foci of activation within the right and left middle fusiform gyrus there was a 96% and 87% overlap with the right and left FFAs respectively. For the area located posterior to the middle fusiform gyrus, in the right hemisphere the right OFAs shared 66% of the total amount of voxels within this region, and in the left hemisphere the overlap (with the left OFA) reached the 92%.

Control experiment: rationale, procedure, analysis and results

One potential caveat of this experiment is that the decrease of the fMRI response at frequencies above 6 Hz for the 'different faces' condition (Fig. 2) could be due to the high repetition rate of the same face identities during a block. Specifically, with a total of 18 faces used in the experiment (see *Stimuli and Procedure* sections) and a block duration of 27 s, each individual face was repeated during the different faces condition a larger amount of times at high than low frequency rates. For instance, since the total amount of faces presented in 6 Hz-different and 12 Hz-different blocks was 162 and 324 faces respectively, a specific face was presented 9 times and 18 times on average, respectively. This could, in principle, give rise, in the latter case, to a lower

fMRI response due to adaptation. In order to rule out this potential account of our observations, we tested six participants (4 of which also participated in the main experiment) in an additional control experiment. The procedure was the same as in the main experiment but we used only blocks of different faces at four different frequency rates: 3, 6, 12 and 20 Hz. The critical manipulation consisted of using in half of the blocks 18 different faces (as in the main experiment) and 36 different faces in the other half. Two runs were recorded for each participant and in each run each condition was repeated 2 times. A GLM analysis within the core of the face-sensitive network (the right OFA, the right FFA, the left FFA and the right pSTS) was performed using 8 predictors (4 frequencies \times 18 or 36 faces). The beta weights related to those predictors (summary statistics) were estimated for each subject ($N = 6$) and were entered as dependent variables the second level analysis. This stage consisted of a repeated-measure ANOVA with number-of-faces (2 levels) and frequency (4 levels) as factors and each subject considered as an independent measurement. We did not find any significant main effect of number-of-faces (the right OFA: $F(1, 5) = 3.247, p = .131$; the right FFA: $F(1, 5) = 1.183, p = .326$; the left FFA: $F(1, 5) = .103, p = .762$; the right pSTS: $F(1, 5) = .508, p = .508$) or interaction between number-of-faces and frequency (the right OFA: $F(1, 5) = .0635, p = .604$; the right FFA: $F(3, 15) = 2.329, p = .116$; the left FFA: $F(1, 5) = .784, p = .521$; the right pSTS: $F(1, 5) = .291, p = .831$) for any of the face-sensitive regions.

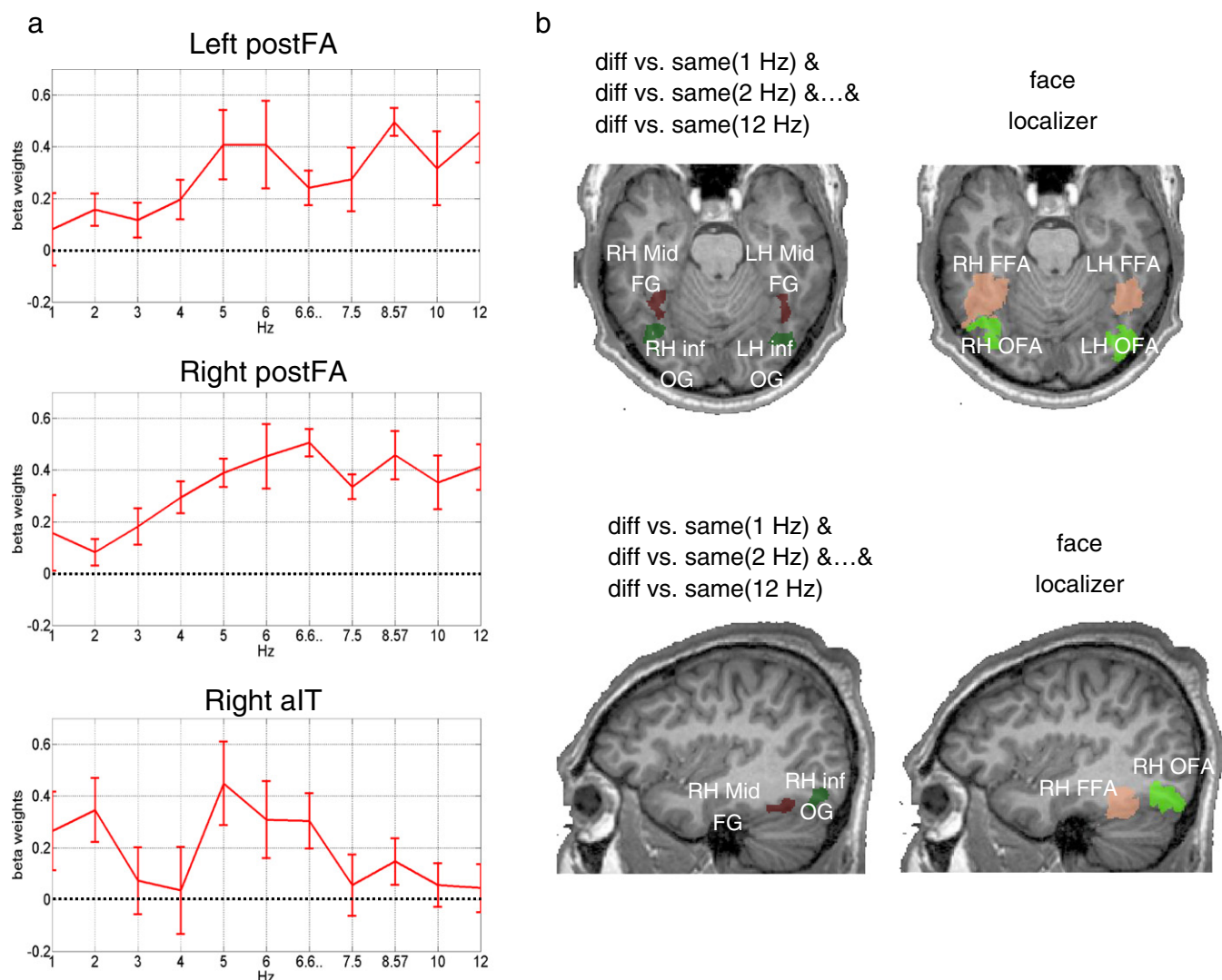


Fig. 5. a) Region of interest analysis related to the 3 additional face-selective areas. b) Whole brain analysis. Comparison between the right/left FFA and right/left OFA localized with the face localizer and the areas activated when performing the conjunction of the contrasts different vs. same at each frequency of stimulation.

In summary, the frequency tuning function of fMRI adaptation in face-sensitive areas of the human brain was characterized by a Gaussian-shaped profile that peaked at an intermediate frequency rate of 6 Hz (i.e., when 6 faces were presented per second). This function was highly similar throughout the face-sensitive areas identified in all individual brains, namely the right OFA, right FFA, right pSTS and left FFA. The strength of this result is underlined by the high frequency resolution of the experimental design (11 frequencies: from 1 to 12 Hz). Moreover, the individual data confirmed that the peak of adaptation at 6 Hz was consistent across subjects. In particular, for most of the subjects (4 out of 6) the adaptation effect peaked at 6 Hz both in the right FFA and OFA. For the remaining two participants it peaked at neighboring frequency rates, namely at 5 and 6.66 Hz (Fig. 4).

Discussion

At first glance, the 6 Hz-peak of the frequency tuning function agrees with previous neuroimaging studies that defined the responses to visual stimuli presented at multiple frequency rates in visual areas. For instance, Ozus et al. (2001) reported an increase of the fMRI activation with stimulus (flash) frequency up to 6 Hz in low-level visual areas. In higher level regions, McKeef et al. (2007) showed a peak of temporal sensitivity between 4.7 Hz and 9.4 Hz in the FFA for face stimuli. In line with this result, Gauthier et al. (2012) recently observed a maximal response in the same area at 5 Hz when alternating face and house stimuli. However, major differences make the comparison between these studies and the present experiment futile: previous studies reported the absolute response to different faces across frequency rates, and in contrast, the frequency tuning function we defined here emerges through the comparison of the two conditions of interest (different vs. same faces). Separately examining these two conditions is necessary to fully understand the frequency tuning of the individual face discrimination function.

The speed of individual face discrimination

The identical fMRI response from 1 to 6 Hz in the ‘different faces’ condition suggests that faces are discriminated equally well when they are presented at 6 Hz and at slower rates (Fig. 2). It means that a face can be fully encoded at the individual level in face-sensitive areas in about 166 ms. Such a fast discrimination rate for individual faces agrees with scalp EEG recordings showing discrimination responses to individual faces at about 160 ms (Heisz et al., 2006; Jacques and Rossion, 2006; Jacques et al., 2007). Moreover, in a recent EEG study, the peak of the frequency tuning function for different faces was also found at about 6 Hz over the right occipito-temporal cortex (Alonso-Prieto et al., 2013). At the neuronal level, a delay of at least 100 ms between a first (target) face and a second (mask) face is necessary to observe two full responses of face-selective neurons in the monkey superior temporal sulcus (STS) (Keysers and Perrett, 2002; Kovacs et al., 1995; Rolls and Tovee, 1995). However, at least 150 ms of evidence accumulation is necessary for fine-grained individuation of faces (Matsumoto et al., 2005; Sugase et al., 1999). If this temporal distance is reduced, the individual face may not be processed at a sufficiently fine-grained level before the next face interrupts, or competes with its processing (Keysers and Perrett, 2002; Keysers et al., 2001). Note that the difference in terms of latency of the neurons’ responses in the monkey brain and the human brain might not be a critical factor here, because we are concerned with the time that is necessary to discriminate faces rather than the absolute latency of response onset.

With regard to the same faces condition, the modulation of the fMRI signal we observed here indicated that when 6 faces or more were presented per second, face-sensitive areas adapted the most. This suggests that for frequencies lower than 6 Hz the interval between two faces is long enough for the system to (partially) recover from the adapted state. In contrast, at 6 Hz populations of neurons appear to be constantly

tuned to the repeated face stimulus, preventing a temporal dispersion of the response. In short, the temporal presentation rate at which individual face discrimination is optimal, namely, at 6 Hz, might prevent the temporal dispersion of the neural response (at too low rates) or the interference (at high rates) between the after-discharge to the first face stimulus and the onset-response to the following one.

Saccadic eye movements

One alternative explanation to the 6 Hz frequency tuning function raised by a reviewer of the present paper is the rate of saccades or microsaccades, which normally acts to ‘refresh’ neural responses, thereby mitigating repetition suppression when the (micro)saccades match the rate of image presentation. Hence, for the same image, there should be less suppression – more refresh – when eye movements can match the image appearance, i.e. below 5 Hz (e.g. Uematsu et al., 2013; see also e.g. Bartlett et al., 2011; Purpura et al., 2003; Rajkai et al., 2008 for studies in macaque monkeys). That is, the visual system would process a stimulus slightly differently than the previous one (different foveal positions). For different faces, that ‘refresh’ would be sufficiently driven by the changes in the visual stimuli (‘exogenous saccades’), therefore there would be a difference when saccades can match the rate of stimuli (<5 Hz) versus when they cannot (>5 Hz). According to this account the 6 Hz tuning function observed would be due to an interaction between passive and active viewing of same and different face stimuli.

Because eye movements were not tracked in the scanner, we cannot rule out this account of our results. However, there are several factors that go against this possibility. First, the subjects were instructed to fixate to a small cross on the nasion of the face (roughly corresponding to the center of the screen) where they performed a task orthogonal to face processing (i.e. color discrimination task) for the entire duration of the block. One reason for this was precisely to minimize the amount of endogenous or exogenous eye movements that could affect the neural adaptation. Second, the subjects were not aware of the manipulation of the experiment (same/different faces). Third, the task was designed to be difficult enough to control that the participants would not disengage from the task by covert attention or by (endogenous or exogenous) saccades. Fourth, there was a large change of the image (size) at every cycle, in both conditions (Fig. 1). Thus, there was an important refresh of the stimulus even for the same faces condition. Fifth, the typical receptive field of face-selective areas is large enough to make the effect described above (for low frequencies) very unlikely to occur. Finally, in a previous EEG study that disclosed the maximal effect at 6 Hz also (Alonso-Prieto et al., 2013), there were no saccadic eye movements recorded and the effect of repetition suppression was not localized on prefrontal regions (generating the saccades). Similarly, our whole brain analysis did not disclose the effects in prefrontal cortex (i.e. frontal eye field) but in face-sensitive areas of the ventral occipito-temporal cortex.

A similar frequency tuning function across face-sensitive brain areas

The high frequency resolution of the present study (11 frequencies ranging from 1 to 12 Hz) was not only designed to draw an accurate profile of face discrimination in terms of (temporal) rates of face presentation. It was also used to potentially reveal different frequency tuning functions in different face-sensitive areas and to gain insight on the temporal evolution of the face discrimination process along the regions of the face-sensitive network. However, contrary to our expectations, all the face-sensitive areas showed the largest effect of face adaption at the same 6 Hz frequency rate, with a qualitatively similar frequency tuning function. This observation suggests that the rate of individual face discrimination is similar in all face-sensitive areas, and that this function may not necessarily occur in a serial/hierarchical manner, e.g., from posterior (i.e., OFA) to higher order areas (Rossion, 2008). It also indicates

that all of the face-sensitive areas contribute to the accumulation of evidence necessary to individualize faces. In this context, we note that most of previous fMRI studies have failed to report any repetition suppression effect to faces in the posterior part of the STS (e.g., [Ewbank and Andrews, 2008](#)), suggesting that this region does not play a role in the coding of identity, at least for static pictures of faces. At low frequency rates, our findings are in agreement with these studies, failing to reveal any adaptation effect in the pSTS when the same face was presented relative to different faces. However, because the pSTS shows neural adaptation effects only in a very narrow frequency range centered around 6 Hz, our data suggest that this region contributes to individualization of faces but has a faster temporal dispersion of its response, possibly due to its specific tuning to rapidly changing (i.e., dynamic) stimuli ([Pitcher et al., 2011](#); [Schultz and Pilz, 2009](#)).

Repetition suppression effects at high frequency rates

A puzzling result of the present experiment concerns the significance of the adaptation effect observed beyond 6 Hz, namely up to 12 Hz. In fact, it is unlikely that the system can process each face identity at such very high frequency rates. As a matter of fact, in a similar EEG experiment differences between different and same faces were not found above a stimulation frequency of 8 Hz ([Alonso-Prieto et al., 2013](#)). One possibility for the adaptation here is that the effects we found at high frequencies (i.e., higher than 8 Hz) in fMRI are due to low-level features of faces (e.g., power spectrum, color), that differ between different faces and to which high-level face-sensitive areas are sensitive to some extent ([Andrews et al., 2010](#); [Rossion et al., 2012](#)). Alternatively, it is possible that at high frequency rates the system bypasses some of the different faces presented in succession, and the effect is driven by the perception of a subset of different faces during a block. This would explain the lack of repetition suppression effect in EEG at high frequencies because with a high temporal resolution frequency-based technique such as EEG, the response to a specific frequency is measured *exactly* at that specific frequency ([Alonso-Prieto et al., 2013](#); [Regan, 1966](#)), while this is not the case with a technique such as fMRI.

Practical implication for fMRI adaptation and behavioral studies

The relevance of the present results has to be considered also in light of the interpretation of previous fMRI adaptation (fMR-A) studies and the design of future studies. In the last ten years fMR-A has been largely used to characterize the response properties of occipito-temporal face-sensitive areas, such as the invariance of representation of face identity, size, rotation and translation ([Andrews and Ewbank, 2004](#); [Grill-Spector and Malach, 2001](#)), the sensitivity to face inversion ([Mazard et al., 2006](#); [Yovel and Kanwisher, 2005](#)) facial expression ([Furl et al., 2011](#); [Winston et al., 2004](#)), the invariance to different levels (high, low) of face spatial filtering ([Eger et al., 2004](#)) or the coding of holistic/configural properties as opposed to part-based representations ([Davies-Thompson et al., 2009](#); [Schultz and Rossion, 2006](#)). Besides their methodological differences, these studies all have in common the relatively low rate at which faces were presented. Across studies, this rate ranged from 0.5 (1 face every 2 s) to 3 Hz (3 faces per second), rates that appears to be suboptimal to disclose large repetition suppression effects. Importantly, in the present experiment, at these temporal frequencies the difference between the fMRI signal related to different and same faces conditions, in most of the cases, did not exceed 0.5% of BOLD signal change. However, when stimulating at around 6 Hz we observed adaption effects almost twice as large. The major implication of this result is that future studies which use repetition suppression to clarify the neural basis of face perception should consider presenting faces at frequency rates around 6 Hz in order to significantly increase the amplitude of the effect to be tested.

In the present experiment, the orthogonal task was also included to investigate the process of face discrimination while controlling for any

attentional effects. However, the lack of any psychophysical measurement on the face stimuli did not allow us to directly test the behavioral relevance of neural adaptation across different rates of face presentation. [Daelli et al. \(2010\)](#), for example, recently showed that, depending on the delay between the images presented, the behavioral consequences of stimulus repetition might either be “attractive” (priming) or “repulsive” (aftereffect). Therefore, it would be of great interest in the future to explore whether the neural adaptation effect we observed here has the same perceptual meaning for each frequency.

Most importantly, if we assume that the amount of neural adaptation is directly correlated with the efficiency of face discrimination, our observations of a frequency tuning function centered on 6 Hz for the cortical face network suggest that this rate might be optimal for behavioral individual face discrimination ([Holcombe, 2009](#)). Above this rate, performance should start to decrease because a given face cannot be fully individualized before the next face comes in and interrupts its processing. Obviously, human observers cannot be expected to perform individual discrimination tasks better at 6 Hz than at slower frequency rates. However, one intriguing possibility is that such an intermediate frequency rate allows one to better isolate the contribution of high-level visual processes than slower rates of stimulation, at which many other factors may contribute to performance. If this is the case, a 6 Hz rate of stimulation in an individual face discrimination task may reduce inter-trial and inter-individual variability in behavioral performance at individual face discrimination, and may potentially be used to characterize abnormal processes in patients suffering from face recognition difficulties.

Finally, the present study used faces because they are an excellent category to test discrimination of exemplars of a visual category. Faces form a visually homogenous set of highly familiar stimuli that are associated with well-defined neural responses. Moreover, unlike other object categories, faces need to be processed beyond a simple category-wise classification (“it’s a face”) into fine-grained subordinate-level discrimination (“it’s face X, not face Y”) in order to ensure adequate social interactions. However, as no other complex visual stimuli (e.g., objects, places or body parts) were used in the present experiment, the specificity of the “6 Hz-effect” to face discrimination remains unknown and should be determined.

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Conflict of interest statement

The authors declare no competing financial interests.

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